ESCHSCHOLZIA COVILLEI GREENE, A TETRAPLOID SPECIES FROM THE MOJAVE DESERT[1]

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The purpose of this paper is to establish the validity of *Eschscholzia covillei* Greene (Papaveraceae) as a taxon of specific rank on the basis of a comparative study of morphological variation in relation to chromosome number and geographical distribution. *Eschscholzia covillei* is one of a group of closely related taxa in the deserts of southwestern United States and adjacent Mexico that has frequently been treated as conspecific with *E. minutiflora* Watson (e.g., Jepson, 1922, 1925; Munz, 1935; Abrams, 1944; Munz, 1959).

Lewis and Snow (1951) pointed out that *E. minutiflora* is hexaploid (n=18) and that a diploid species, *E. parishii* Greene (n=6), formerly considered a variety of *E. minutiflora*, is readily distinguishable from the latter on morphological grounds. They also pointed out that plants intermediate between these two taxa in Inyo County, California, might be tetraploid and genetically distinct from both *E. minutiflora* and *E. parishii*. This suggestion was confirmed in 1957 when a collection of the intermediate material from the White Mountains (*Lewis 1084*) was determined to be tetraploid (n=12). More recently Ernst (1959) has reported the tetraploid number of chromosomes for two collections from the same area (*Ernst 561*, *564*). From study of my own collections, I have found that these intermediate specimens are consistently tetraploid and morphologically distinguishable from both the diploid, *E. parishii*, and the hexaploid, *E. minutiflora*. Consequently the tetraploid should be recognized as a distinct species. An examination of the literature and of the type specimens concerned indicates that the earliest specific name for the tetraploid is *E. covillei* Greene. This was clearly designated on the United States National Herbarium sheet (number 3340) by Greene.

ESCHSCHOLZIA COVILLEI Greene, Pittonia 5:275. 1905. Type: from Pete's Garden to 1000 feet below, Johnson Cañon, Panamint Mountains, Inyo County, California, elevation 1700 meters, *Coville & Funston 519* (US). *E. minutiflora* var. *darwinensis* M. E. Jones, Contr. West. Bot. 8:2–3, 1898. Type: on mesas, Darwin, Inyo County, California, *Jones* in 1897 (POM).

Glabrous annual herb, to 40 cm. tall, freely branched throughout; basal rosettes well-developed with leaves coarsely divided, numerous,

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glaucous, 6–13 cm. long, the blade 0.5–4.5 cm. long, 0.5–4 cm. wide; upper leaves strongly reduced; mature buds elliptical, 6–9 mm. long, acuminate; pedicels 1–8 cm. long; torus turbinate; petals obovoid-cuneate, golden-yellow, 7–17 mm. long; stamens 8–15 per flower, 3.5–5 mm. long; pollen with 7–10 grooves (usually 8 or 9), 24–37 microns in diameter; seeds with finely reticulate grey-brown coat; chromosome number, $n = 12$.

Distribution. Slopes and washes of desert mountains, Inyo and San Bernardino counties, California (fig. 1).

Representative specimens. CALIFORNIA. Inyo County: Panamint Valley, 11 miles southwest of Ballarat on road to Ridgecrest, *Mosquin* & *Lewis 3241* (LA, UC); 0.7 mile from junction to Darwin on road to Darwin Falls, *Mosquin* & *Lewis 3251* (LA, UC); Panamint Valley, 7.2 miles east of junction to Trona on road to Stovepipe Wells, *Mosquin* & *Lewis 3255* (LA, UC); Emigrant Canyon, *Mosquin* & *Lewis 3256*, *3257* (LA, UC); 0.6 mile west of Bradbury Well entrance to Death Valley National Monument, *Mosquin* & *Lewis 3258–1* (UC); Westgard Pass road, *Lewis 1084* (LA); Nelson Range, *Austin* in 1906 (UC); Pleasant Canyon, Panamint Mountains, *Hall* & *Chandler 6965* (UC); Hole-in-the-Rock Spring, *Epling* et al. in 1930 (LA, UC); Hanaupah Canyon, Panamint Mountains, in 1922 (collector unknown, SD); Shepherds Canyon, Argus Mountains, *Keller 126* (SD); Black Canyon, White Mountains, *Duran 2668* (LA, UC); Bishop Creek, 5,200 feet, *Hall* & *Chandler 7249* (UC); Darwin, 4,600 feet, *Jones*, April 28, 1897 (POM); from Pete's Garden to 1000 feet below, 1,700 meters, *Coville* & *Funston 519* (US). San Bernardino County: 7 miles east of Daggett, *Munz* & *Keck 7843* (POM); 10 miles southwest of Garlic Springs, *Munz* & *Keck 7878* (POM).

Eschscholzia covillei is usually readily distinguishable from *E. minutiflora* (table 1), especially when the two are found in adjacent or mixed colonies. Where they occur in mixed colonies the two are distinguished by flower size and habit. It is perhaps more difficult to distinguish *E. covillei* from *E. parishii*, but the two are not known to grow together (fig. 1). In general, the latter two differ consistently in stamen number and in the number of grooves on the pollen. The specimens from San Bernardino County that are identified as *E. covillei* are geographically closest to *E. parishii* and it would be desirable to have additional chromosome number determinations from this area in order to confirm their identification. The hexaploid species, *E. minutiflora*, also grows sympatrically with *E. parishii*, and in such localities plants of the two species are readily distinguished, as is also true of most herbarium specimens, by the larger flowers and greater stamen number of *E. parishii*. All three species are found on comparatively moist alluvial slopes and fans, but unlike the other two species, the hexaploid *E. minutiflora* extends onto the desert floor.

Plants of *Eschscholzia parishii* from near Randsburg, Kern County (*Lewis* & *Mosquin 1117*; *Heller 7683*), the only locality for this species on the Mojave Desert, are intermediate in several morphological traits between *E. parishii* from the Colorado Desert and *E. covillei*. They may have as few as 14 stamens per flower, and they have an intermediate pollen morphology and stamen number. In the Heller collection, pollen

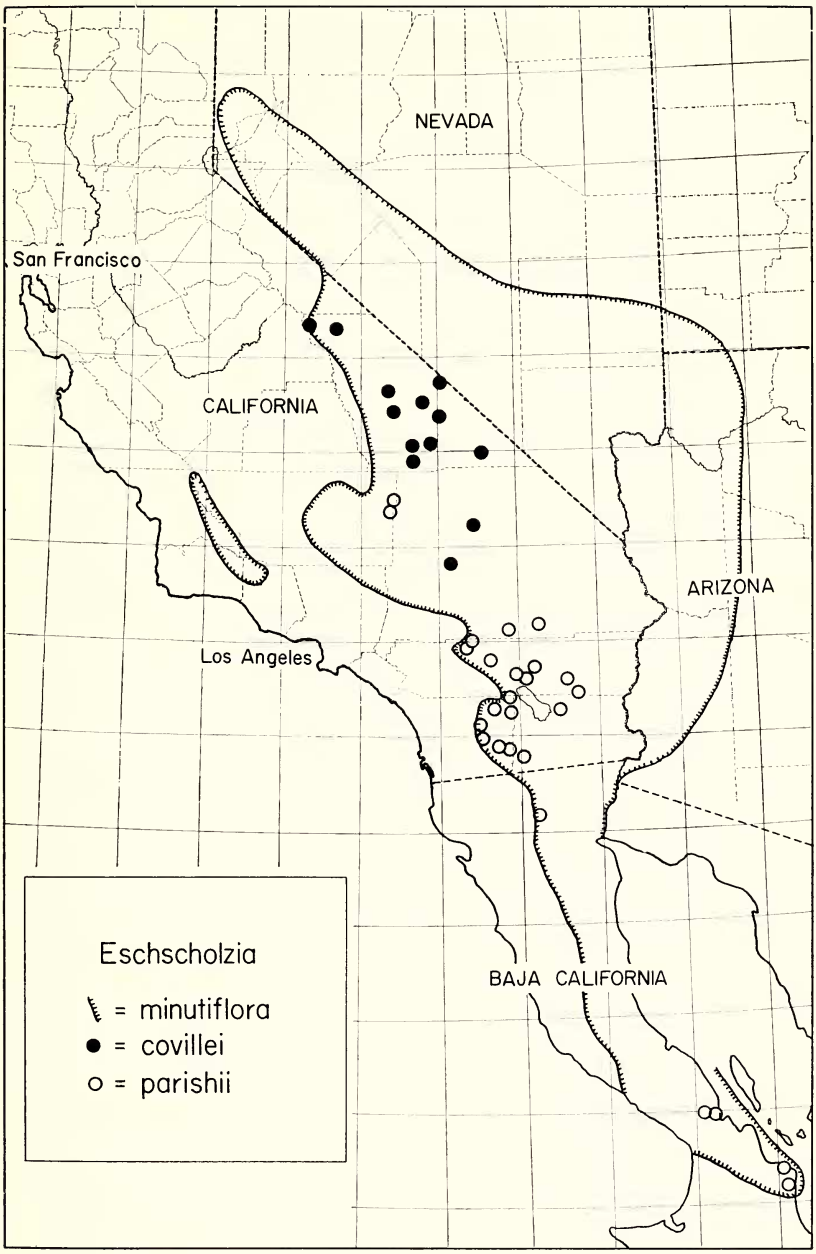

Fig. 1. General distribution of *Eschscholzia minutiflora* and selected localities of *E. covillei* and *E. parishii*.

size varied from 17–21 microns, and the two buds examined had, respectively, 14 and 15 stamens. The pollen had 7 and 8 grooves in approximately equal frequencies. In the Lewis and Mosquin collection, for which the chromosome number has been determined, pollen diameter varied from 20–32 microns, the pollen had 7, rarely 6, grooves per grain, and the stamen number varied from 16–18 per flower. In view of these morphological traits this might be considered a local subspecies of *E. parishii*.

The chromosomes of all three species are similar in size and morphology, with ring bivalents being more frequent than rods. The following list includes all known chromosome counts[2] made in this group:

Eschscholzia parishii (n = 6). California. Kern County: about 2 miles southeast of Searles Station, *Lewis & Mosquin 1117* (3 plants, 1 count from somatic cells). Riverside County: Morongo Wash, *Snow 11* (5 plants)[a]; about 5 miles west of road to Cottonwood Springs on United States Highway 60, *Lewis & Ernst* in 1949 (3 plants)[b]; Joshua Tree National Monument, *Lewis* in 1949[b]; Box Canyon, *Snow 7*[a]; *Raven 11478* (somatic count).

Eschscholzia covillei (n = 12). California. Inyo County: *Mosquin & Lewis 3241* (2 plants), *3251* (3 plants), *3255–3, 3255–4* (2 plants), *3256* (2 plants), *3258–1*; *Lewis 1084*; Westgard Pass road, 2.8 miles west of Zurich, *Ernst 561*[d], 1.6 miles west of Zurich, *Ernst 564*[d].

Eschscholzia minutiflora (n = 18). California. Imperial County: road to 17 Palms, 0.3 miles east of United States Highway 99, *Lewis* in 1952. Inyo County: Panamint Valley, 15 miles north of road to Darwin on road to Stovepipe Wells, *Mosquin & Lewis 3240*; 4.6 miles from junction of State Highway 190 with road to Darwin Falls, *Mosquin & Lewis 3249, 3250* (total of 3 plants); 4.2 miles north of road to Darwin Falls on road to Darwin Springs, *Mosquin & Lewis 3254*; Panamint Valley, 7.2 miles east of junction to Trona on road to Stovepipe Wells, *Mosquin & Lewis 3255–1, 3255–2* (2 plants); 0.6 mile west of Bradbury Well entrance of Death Valley Natl. Mon., *Mosquin & Lewis 3258–2*; east of Darwin, *Snow 26* (approximate count)[a]; just below Darwin Falls, *Raven 12114*. Kern County: 2 miles southeast of Searles Station, *Lewis & Mosquin 1117–4*. Los Angeles County: 0.5 mile north of Pearblossom, *Mosquin 3265*. Riverside County: about 5 miles west of road to Cottonwood Springs on United States Highway 60, *Lewis & Ernst* in 1949 (3 plants)[b]; road to Cottonwood Springs, 7.2 miles north of United States Highway 60, *Snow 10*[a]; Box Canyon, *Snow 51*[a]. San Bernardino County: 0.8 mile north of Atolia, *Lewis* in 1950[b]; about 2 miles west of Lucerne Valley, *Snow 12*[a]; 10.2 miles east of Barstow, *Snow 23*[a]; United States Highway 395, 22 miles south of Inyo County line, *Snow 25–1*[a]; 15.9 miles south of Kramer Junction, *Lewis & Mosquin 1114*; 2 miles north of Needles, *Raven 13891* (approximate count). San Diego County: Mason Valley, near Vallecito Station, *Ernst 258*[c]. Baja California, Mexico. 14.8 miles south of Mexican Highway 2 on road to San Felipe, *Raven 11630*.

Eschscholzia minutiflora also occurs in the South Coast Ranges of California (*Axelrod 260*, UC; *Axelrod 9170*, POM; *Schreiber 1045*, UC). The identification of this species is based on morphological considera-

[2] Counts by Snow (unpublished) indicated by [a], those of Lewis & Snow, by [b], those of Ernst, 1958, by [c], and those of Ernst, 1959, by [d]. Vouchers for chromosome number determinations not previously reported are on file in the herbarium, University of California, Berkeley, or in the herbarium, University of California, Los Angeles. The first set of my own collections are deposited at the herbarium of the University of California at Berkeley.

Table 1. Morphological Comparison of Three Species* of Eschscholzia

	E. parishii (n=6)	*E. covillei* (n=12)	*E. minutiflora* (n=18)
Habit (rosette)	Poorly developed	Well developed	Well developed (Colorado Desert) or lacking (Mohave Desert)
Habit (branching)	Slender, delicate	Much-branched	Much-branched
Length of longest petals (range in mm.)	8–22	7–18	4–10
Length of mature buds (range in mm.)	7–16	6–9	2–7
Bud apex	Acuminate	Acuminate	Blunt (Colorado Desert or acuminate (Mohave Desert)
Number of stamens (range)	16–37	8–15	4–15
Length of longest stamens (range in mm.)	4–7.5	3.5–5	2–4
Number of pollen grooves** (range of means)	5.5–7	7.5–9.1	8.2–10.4
Diameter of pollen (range in microns)	20–32	24–37	25–44

* Only considering plants from which the chromosome number has been determined, 9 of *E. parishii*, 12 of *E. covillei*, and 27 of *E. minutiflora*.

** Mean of each plant based on 10 grains.

tions. One plant (*Axelrod 9170*) which was examined in detail had only 10 stamens per bud, a pollen diameter of 40 to 44 microns and usually 11 rarely 10 grooves per pollen grain. I have examined the pollen of the diploids *E. californica* Cham., *E. caespitosa* Benth., *E. glyptosperma* Greene, and *E. californica* var. *peninsularis* (Greene) Munz, and have found these plants to have a pollen variation comparable to *E. parishii* and out of the range of the pollen of *E. minutiflora*. A comparison of the pollen traits of *E. minutiflora* in the South Coast Range to those of *E. parishii* as shown in table 1 can leave little doubt that these Coast Range plants are hexaploid. The presence of this desert hexaploid in dry areas of the South Coast Ranges is not too surprising for a similar pattern of distribution is known for other desert annuals, e.g. *Linanthus parryae* (Gray) Greene, *Streptanthella longirostris* (Wats.) Rydb., *Erio-*

gonum trichopes Torr., *Chaenactis xantiana* Gray and *Salvia columbariae* Benth.

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ABNORMAL FRUITS AND SEEDS IN ARCEUTHOBIUM[1]

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The normal *Arceuthobium* fruit, as described in the literature (Thoday and Johnson 1930, Dowding 1931, Gill 1935, Kuijt 1955, 1960), consists of a single seed containing one embryo. This paper describes abnormal fruits with two seeds and seeds with two embryos and endosperms as found in some specimens of *A. americanum* Nutt. ex Engelm. and *A. vaginatum* f. *cryptopodum* (Engelm.) Gill.

The fruit of *Arceuthobium* and other members of the Loranthaceae differs from other angiosperms in that there are no true ovules. The ovarian cavity becomes nearly filled by an undifferentiated mound of tissue termed the mamelon, nipple, or ovarian papilla. Two embryo sacs are borne within the ovarian papilla. Usually only one embryo sac develops, but occasional diembryonic seeds have been reported in a number of species (Peirce 1905, Weir 1914, and Heinricher 1915). The process of fertilization in *Arceuthobium* has not been precisely described. However, the development of the embryo sac after fertilization is apparently similar to that in most dicotyledonous plants. As the fruit matures, the dominant embryo sac develops into a copious endosperm with a small embryo. The remnants of the ovarian papilla become crushed, and in *A. pusillum* they form a distinct "crest" at the base of the seed (Thoday and Johnson 1930). The crest was not well defined in the mature, normal *A. americanum* (fig. 1A) and *A. vaginatum* f. *cryptopodum* fruits examined. However, a small mass of tissue which is presumed to be analogous to the

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